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The Food of Cod in Icelandic Waters

By BENNET B. RAE
Marine Laboratory, Aberdeen
July 1968

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The Food of Cod in Icelandic Waters

INTRODUCTION

Notes on the food of cod were recorded on Scottish research vessel surveys of Icelandic waters from September 1952 to August 1958, when the stomach contents of nearly 3,000 cod and codling of 21 cm and over were examined from 119 trawl catches. Sampling of the catches was carried out as other requirements of the programme and circumstances permitted, so that not all the cod caught were examined. Samples varied from 1 to 146 fish, including 59 of fewer than 10 fish, 37 of 10 to 50 fish, 17 of 51 to 100 fish, and 6 of 101 to 146 fish, and thus covered a considerable range of cod concentrations. Where possible all cod were dealt with, but in very large catches samples representative of the size range were examined.

Research cruises to Iceland were confined to the seven months from March to September and sampling was most extensive in April, May, July and September (Table I). Stomachs were examined from each locality investigated around the entire coastline and offshore, in some places, to a distance of 50 miles. No fishing was carried out within three miles of the coast at any point. The numbers of cod of 21 to 50 cm and of 51 cm and over examined in each statistical rectangle are given in Figure 1. Though variable, the numbers in each size-group may be regarded as reasonably representative of cod stocks in Icelandic waters.

As in similar investigations in Scottish and Faroese waters, the stomach contents were examined on board ship during the routine treatment of each trawl catch. Emphasis was placed on the recognition of the chief food types—phylum, class or genus—and little attempt was made to identify the various species unless these were in fairly good condition and readily recognisable. A list of the genera and species identified in the various localities is given in the appendix. In the circumstances no quantitative measurements of the food were attempted, but, as observed in previous studies of the food of Scottish and Faroese cod, the frequency of occurrence of the main food types may be regarded as giving a reasonably close representation of their relative quantitative values.

SEASONAL INTENSITY OF FEEDING AT ICELAND

On the assumption that the proportions of fish with food in their stomachs month by month reflect the intensity of feeding at different times of the year, the numbers of cod examined and the numbers with empty stomachs in each of the two size-groups are set out in Table I. It is unfortunate that no observations have been possible during the winter so as to provide a comparison with similar results from Scottish and Faroese waters.

In the smaller size-group, 21–50 cm, the proportions of fish with empty stomachs varied only slightly (21–25%) from April to September. In the larger size-group, 51 cm and over, the proportion of fish with no food in their stomachs ranged from 45 to 58% from March to May, and from 19 to 24% from June to September.

These results suggest that the intensity of feeding of the smaller and predominantly immature or adolescent fish varies little throughout the period investigated. The mainly adult fish of 51 cm and over, however, fed most intensively from June to September, while nearly half of this size category examined from March to May had empty stomachs. The overall figures for all sizes of Icelandic cod from March to September reveal a much higher proportion of fish with empty stomachs than in Scottish and Faroese waters (Table II).

The Icelandic results also differ from those of the other two regions in not showing the marked decline in the feeding of cod during the spring—in March and April (Scotland) and May (Faroe)—which has been linked with the spawning period in each of these regions.

The degree of fullness of most of the cod stomachs was also noted. These observations on cod of all sizes, summarised in Table III, again reveal the relatively high proportions of empty stomachs during the spring

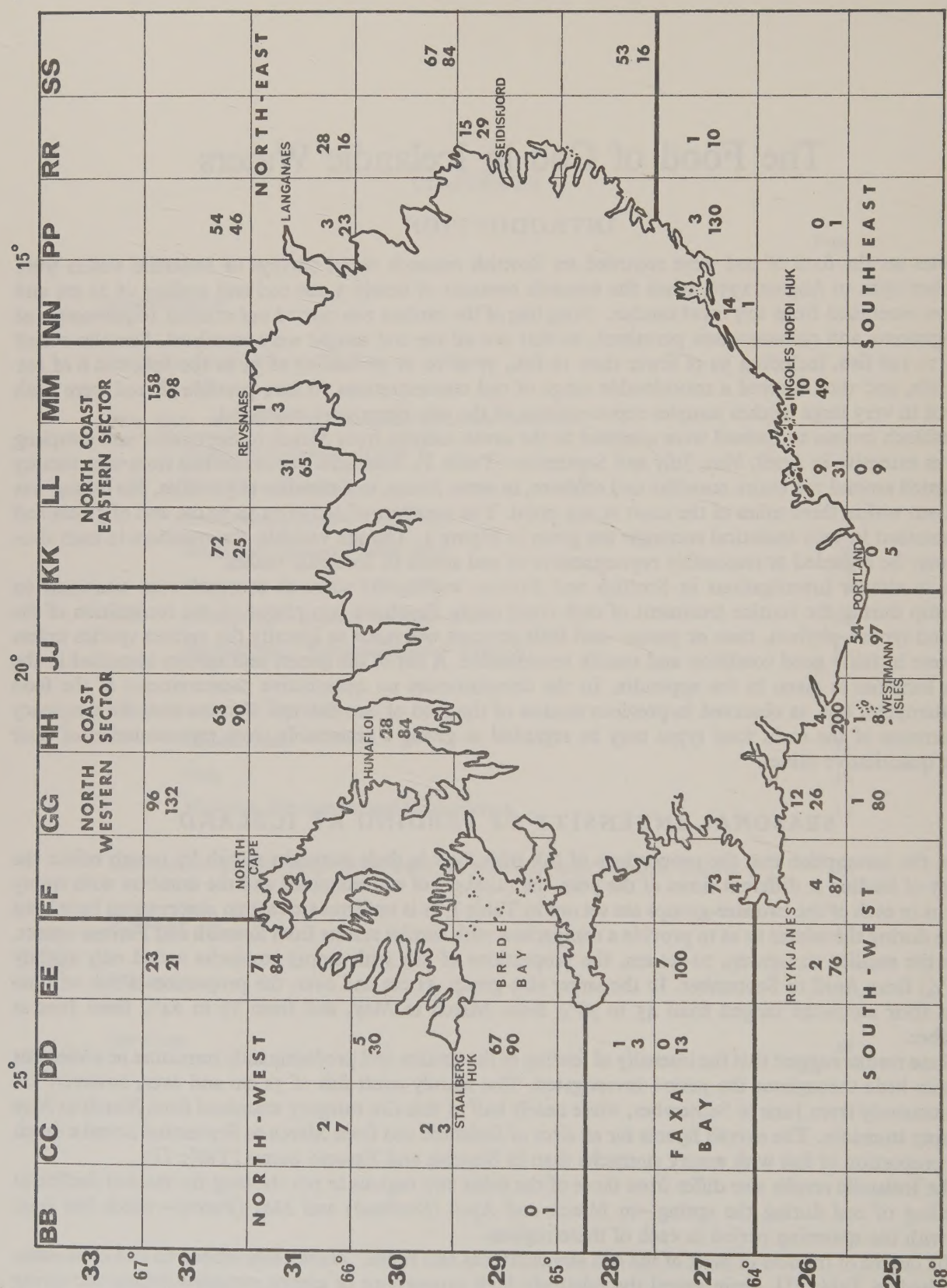

Figure 1. Sampling of cod stomachs at Iceland 1952–1958; upper figure = number of cod of 21–50 cm, lower figure = number of cod of 51 cm and over.

TABLE I

FEEDING OF COD AT ICELAND, 1952–1958
NUMBERS EXAMINED AND NUMBERS WITH EMPTY STOMACHS (ALSO EXPRESSED AS PERCENTAGES)

Month	Years	21–50 cm No. Exam.	21–50 cm No. Empty	21–50 cm %	51–135 cm No. Exam.	51–135 cm No. Empty	51–135 cm %	Totals No. Exam.	Totals No. Empty	Totals %
March	1958	1	1	—	74	43	58	75	44	59
April	1957–58	13	3	23	641	288	45	654	291	44
May	1955–57	287	61	21	248	120	48	535	181	34
June	1953–57	9	2	22	25	5	20	34	7	21
July	1957–58	467	116	25	505	121	24	972	237	24
August	1956	1	0	—	27	5	19	28	5	18
September	1952–57	251	52	21	394	86	22	645	138	21
March–May		301	65	22	963	451	47	1264	516	41
June–August		477	118	25	557	131	24	1034	249	24
September		251	52	21	394	86	22	645	138	21
March–September		1029	235	23	1914	668	35	2943	903	31

TABLE II

COMPARISON OF PROPORTIONS OF COD WITH EMPTY STOMACHS
IN SCOTTISH, FAROESE AND ICELANDIC WATERS

Region	Months of Sampling	Size Groups 21–50 cm No. Exam.	21–50 cm No. Empty	21–50 cm %	51 and over No. Exam.	51 and over No. Empty	51 and over %	Total No. Exam.	Total No. Empty	Total %
Scottish	I–XII	5920	986	16·7	4704	796	16·9	12918*	2275	17·6
Faroese	I–XII	2193	341	15·5	2021	340	16·8	4214	681	16·2
Icelandic	III–IX	1029	235	22·8	1914	668	34·9	2943	903	30·7

*including 2294 examined, 493 empty, of various unknown sizes

TABLE III

INTENSITY OF FEEDING OF COD OF ALL SIZES ON ICELANDIC GROUNDS

Year	Month		Empty	Traces	¼ full	½ full	¾ full	Full	Total
1956	September		78	48	84	48	16	10	284
		%	27	17	30	17	6	3	
1957	April		205	8	33	39	22	59	366
		%	56	2	9	11	6	16	
1957	May		148	150	109	83	9	2	501
		%	30	30	22	16	2	+	
1957	June		3	3	4	4	2	3	19
		%	16	16	21	21	10	16	
1957	July		232	268	209	145	37	47	938
		%	25	29	22	15	4	5	
1957	September		36	74	70	42	14	15	251
		%	14	29	28	17	6	6	
1958	March		44	3	10	2	3	13	75
		%	59	4	13	3	4	17	
1958	April		86	20	47	37	9	89	288
		%	30	7	16	13	3	31	
1958	July		5	5	2	8	11	3	34
		%	15	15	6	23	32	9	

and the relatively low proportions from June to September. They also show, however, that the highest proportions of full stomachs was in April 1958 (31%) and that full stomachs were also prominent in March 1958 (17%) and April 1957 (16%). These latter results may appear to disagree with the high percentages of cod with empty stomachs in March and April in Table I, but by condensing Table III as in Table IV it becomes evident that feeding generally is at its lowest intensity in May and at its highest in June. Moreover, in March and April, it would appear from the proportions of cod with stomachs empty or less than half-full and of those more than half-full that the intensity of feeding is not unlike that in July and September. It seems likely, therefore, that the feeding cycle of cod at Iceland may be closer to that of Scottish and Faroese waters than Table I shows, and that feeding possibly falls to a minimum, at least among adult fish, in the spring during the spawning period, before rising to a maximum in June and perhaps July.

TABLE IV

SUMMARY OF RESULTS IN TABLE III

	Total	Empty and less than ½ full		More than ½ full	
		No.	%	No.	%
March	75	57	76	18	24
April	654	399	61	255	39
May	501	407	81	94	19
June	19	10	53	9	47
July	972	721	74	251	26
September	535	390	73	145	27

TABLE V

FOOD OF COD OFF NORTH-WEST ICELAND

BB29; CC30, 31; DD29, 30; EE31, 32

Year	1957				
Months	V, VII, IX				
Depth range m	42–146				
Length range cm	26–50	51–128			
No. stomachs examined	170	236			
No. empty	29 = 17%	98 = 42%			
No. with recognisable food	141 = 83%	138 = 58%			
Percentage containing:					
CRUSTACEA	59	53	PISCES	65	62
Decapoda ? sp.	6	—	*Ammodytes*	16	33
Eupagurus	4	5	*Gadus* ? sp.	7	4
Hyas	13	15	*G. merlangus*	1	2
Lithodes	—	1	*G. esmarkii*	11	8
Nephrops	—	1	Flatfish ? sp.	3	1
Galathea	1	1	*Hippoglossoides*	1	2
Munida	2	5	*Lumpenus*	1	1
Crangon	7	1	MOLLUSCA	3	7
Pandalus	18	18	Gasteropoda	1	3
Pontophilus	2	—	*Buccinum*	—	1
Spirontocaris	2	—	Lamellibranchiata	—	4
Hippolyte	4	1	*Modiolus*	—	1
Euphausiacea	4	14	POLYCHAETA	3	4
Isopoda	—	1	*Aphrodite*	—	1
Amphipoda	2	1	GEPHYREA	—	1
OPHIUROIDEA	2	4	PORIFERA	1	—

THE FOOD OF COD IN THE VARIOUS ICELANDIC REGIONS

The results of this investigation have been considered on a regional basis, partly for geographical reasons and partly on account of the nature of the chief constituents of the cod food.

North-west Iceland (Table V)

This area was sampled in May and from July to September of 1957. The food of cod of all sizes consisted predominantly of crustaceans and fish and these types were represented mainly by *Pandalus*, *Hyas*, *Ammodytes* and small gadoids, especially *Gadus esmarkii*. It addition the larger cod preyed fairly frequently on euphausiids, but molluscs, polychaetes and echinoderms were of relatively minor importance to both size-groups.

Faxa Bay (Table VI)

In this area, which was sampled from April to September in 1953 and 1957, a high proportion of the stomachs was empty. Fish were the outstanding food for all sizes of cod. Crustaceans in the form of *Pandalus* and *Crangon* were eaten mainly by the smaller cod. Among the fish eaten, sand eels were outstanding in the diet of both size-groups in July and capelin were eaten fairly frequently by the larger cod in April. Molluscs, polychaetes and echinoderms were unimportant.

TABLE VI

FOOD OF COD IN FAXA BAY AREA

DD27, 28; EE27; FF27

Years	1953, 1957				
Months	IV, VI, VII, IX				
Depth range m	35–156				
Length range cm	29–50	52–114			
No. stomachs examined	81	157			
No. empty	26 = 32%	111 = 71%			
No. with recognisable food	46 = 57%	45 = 28%			
No. with unrecognisable food	9 = 11%	1 = 1%			
Percentage containing:					
CRUSTACEA	28	9	PISCES	80	91
Decapoda ? sp.	2	—	*Ammodytes*	28	47
Portunus	2	—	*Mallotus*	—	16
Nephrops	—	4	*Gadus aeglefinus*	—	2
Munida	2	—	*G. poutassou*	—	2
Pandalus	7	2	*Clupea harengus*	—	4
Hippolyte	2	—	MOLLUSCA	2	4
Crangon	9	—	Gasteropoda	2	2
POLYCHAETA	2	2	Lamellibranchiata	—	2
Aphrodite	—	2			

South-west Iceland (Table VII)

This area, stretching from Reykjanes to Portland, was sampled from March to September in five different years. Most of the fish examined were of the larger size-group. Pandalids and crangonids were the chief items in the diet of the smaller cod, while capelin (mainly in April), sand eels (mainly in September) and *Nephrops norvegicus* were outstanding in the food of the larger cod. Once again molluscs, polychaetes and echinoderms were seldom identified in the stomachs.

Meschkat (1936) studied the stomach contents of 1,245 cod caught in this region (near the Westmann Isles), in February and March 1935. Although the sizes of his cod were not disclosed his identifications of their food are interesting in showing crustaceans and fish to be the predominant types with *Crangon*, *Pandalus*,

TABLE VII

FOOD OF COD OFF SOUTH-WEST ICELAND

EE26; FF26; GG25, 26; HH25, 26; JJ25

Years	1952–53, 1955, 1957–58				
Months	III–VII, IX				
Depth range m	46–176				
Length range cm	24–50	51–135			
No. stomachs examined	78	574			
No. empty	25 = 32%	235 = 44%			
No. with recognisable food	53 = 68%	321 = 56%			
Percentage containing:					
CRUSTACEA	17	18	PISCES	85	86
Eupagurus	—	1	*Ammodytes*	68	12
Portunus	—	+	*Mallotus*	—	53
Nephrops	—	16	*Gadus esmarkii*	4	5
Galathea	—	+	*G. poutassou*	—	1
Crangon	6	1	Flatfish ? sp.	—	+
Pandalus	9	2	*Hippoglossoides*	2	2
Meganyctiphanes	—	+	*Clupea harengus*	—	1
MOLLUSCA	2	+	*Argentina*	—	+
Lamellibranchiata	2	—	POLYCHAETA	—	+
Cephalopoda	—	+	*Aphrodite*	—	+
OPHIUROIDEA	—	1			

Schizopoda, *Nephrops*, *Portunus*, *Mallotus* (capelin), *Argentina*, *Ammodytes*, *Aphrodite* and the brittle-star *Ophiura*, as the outstanding subtypes. Capelin proved to be the commonest single fish type in the food and were eaten more than twice as frequently as sand eels. The prominence of capelin in the diet of Icelandic cod in the early spring is explained by the dense shoals which at this time approach the coast of Iceland to spawn (Saemundsson, 1949).

South-east Iceland (Table VIII)

Sampling from April to September in three different years showed that the cod stock of this region, like that of the previous region, consisted predominantly of large fish. The smaller size-group was found to be feeding on a variety of crustaceans, including *Pandalus*, *Crangon*, *Hyas* and euphausiids and on the inshore fish *Lumpenus*, while the larger cod preyed heavily on capelin in April and less intensively on *Nephrops*, small gadoids and flatfishes at other times. As in the regions already considered, molluscs, echinoderms and polychaetes formed a relatively insignificant part of the cod food.

North-east Iceland (Table IX)

In this area, investigated from May to September in 1956 and 1957, small codling were much more numerous than on the south coast and both size-groups were equally well sampled. In contrast to the four regions considered so far, crustaceans were the commonest food of both size-groups of cod with fish a close second in the diet of the larger fish. Though molluscs were still of little importance in the diet, both polychaetes and echinoderms were eaten by much higher proportions of all sizes of fish than on any of the previous grounds. Among the individual subtypes euphausiids were eaten in some quantity and more frequently by both size-groups than on any of the other grounds. Reptant decapods, particularly *Hyas*, were well represented in the stomachs but natant types, such as *Pandalus* and *Crangon*, were surprisingly of little importance. Although at least 12 species of fish were identified in the food of cod from this region, only long rough dabs (by 6% of the larger fish) and herring (by 5%) were taken in any quantity. Despite the relatively high proportion of cod feeding on polychaetes (22% of the smaller and 10% of the larger fish), *Aphrodite*, which is such a prominent

TABLE VIII

FOOD OF COD OFF SOUTH-EAST ICELAND

KK25; LL25, 26; MM26; NN27; PP26, 27; QQ27

Years	1952, 1956–58				
Months	IV, VI–IX				
Depth range m	73–179				
Length range cm	26–50	51–130			
No. stomachs examined	37	236			
No. empty	9 = 24%	40 = 17%			
No. with recognisable food	28 = 76%	196 = 83%			
Percentage containing:					
CRUSTACEA	71	14	PISCES	43	91
Decapoda ? sp.	—	1	*Mallotus*	—	74
Hyas	18	—	*Gadus* ? sp.	4	—
Portunus	4	—	*G. esmarkii*	4	5
Nephrops	4	10	*G. poutassou*	—	3
Munida	4	1	*Onos cimbrius*	—	1
Crangon	11	—	Flatfish ? sp.	—	4
Pandalus	21	4	*Hippoglossoides*	4	—
Euphausiacea	18	—	*Clupea harengus*	—	1
Meganyctiphanes	11	—	*Lumpenus*	11	—
Cirripedia	4	—	POLYCHAETA	—	1
MOLLUSCA	4	3	*Aphrodite*	—	1
Lamellibranchiata	—	1	HOLOTHUROIDEA	—	1
Cephalopoda	—	1	ASCIDIACEA	—	1

TABLE IX

FOOD OF COD OFF NORTH-EAST ICELAND

PP31, 32; QQ29, 31; RR28, 30

Years	1956–57				
Months	V, VII, IX				
Depth range m	64–154				
Length range cm	23–50	51–105			
No. stomachs examined	220	214			
No. empty	51 = 23%	32 = 15%			
No. with recognisable food	159 = 72%	176 = 82%			
No. with unrecognisable food	10 = 5%	6 = 3%			
Percentage feeding on:					
CRUSTACEA	73	59	PISCES	26	49
Decapoda ? sp.	2	1	*Ammodytes*	1	—
Eupagurus	1	4	*Mallotus*	2	2
Hyas	7	5	*Gadus* ? sp.	—	3
Crangon	1	1	*G. aeglefinus*	—	1
Pandalus	—	2	*G. merlangus*	1	—
Pontophilus	—	1	*G. esmarkii*	—	1
Sabinea	—	1	*G. callarias*	1	1
Sclerocrangon	1	—	Flatfish ? sp.	—	3
Euphausiacea	40	44	*Hippoglossoides*	—	6
Amphipoda	5	3	*Clupea harengus*	1	5
Isopoda	—	1	*Anarhichas*	—	1
MOLLUSCA	1	6	*Lumpenus*	1	4
Gasteropoda	—	2	*Lycodes*	—	1
Lamellibranchiata	1	3	*Triglops*	1	—
Cephalopoda	—	1	ECHINODERMATA	16	17
POLYCHAETA	22	10	Holothuroidea	13	12
Aphrodite	—	1	Ophiuroidea	3	10
NEMERTEA	1	2	ANTHOZOA	—	2
GEPHYREA	1	1			

item in the food in Scottish waters, was found in only one per cent of the stomachs of the larger cod. Most of the echinoderms found in the stomachs of cod of all sizes consisted of unidentified holothurians, but ophiuroids were also prominent in the food of the larger fish.

The prominence of euphausiids, polychaetes other than *Aphrodite*, holothurians and ophiuroids in the food of cod from this region is in agreement with the results of Brown and Cheng (1946) who obtained many of their cod stomachs from north-east Iceland.

TABLE X

FOOD OF COD OFF THE NORTH COAST OF ICELAND—EASTERN SECTOR

KK32; LL31; MM31, 32

Years	1956–57				
Months	V, VII, IX				
Depth range m	68–170				
Length range cm	21–50	51–93			
No. stomachs examined	262	191			
No. empty	45 = 17%	46 = 24%			
No. with recognisable food	210 = 80%	139 = 73%			
No. with unrecognisable food	7 = 3%	6 = 3%			
Percentage feeding on:					
CRUSTACEA	87	53	PISCES	25	65
Eupagurus	1	—	*Ammodytes*	1	7
Hyas	2	4	*Mallotus*	6	4
Crangon	+	—	*Gadus* ? sp.	1	9
Pandalus	6	18	Flatfish ? sp.	—	2
Pontophilus	+	1	*Hippoglossoides*	1	2
Euphausiacea	55	19	*Clupea harengus*	—	1
Meganyctiphanes	53	12	*Lumpenus*	+	6
Amphipoda	5	1	*Lycodes*	+	5
Isopoda	1	1	*Triglops*	1	—
POLYCHAETA	3	4	ECHINODERMATA	1	1
Aphrodite	—	1	Holothuroidea	—	1
NEMERTEA	—	1	Ophiuroidea	1	—
CTENOPHORA	—	1			
Beroe	—	1			

North Coast—Eastern Sector (Table X)

Small codling were plentiful in this area which was sampled from May to September in 1956 and 1957. The food of the smaller size-group consisted chiefly of crustaceans, with euphausiids (mainly *Meganyctiphanes*) the outstanding subtype. In the food of the larger size-group crustaceans were again prominent, but fish were the dominant type. Of the crustaceans, *Pandalus* and euphausiids were outstanding, while the fish diet included at least seven species, each occurring in from 1 to 9% of the stomachs. In this region molluscs were identified in none of the stomachs, polychaetes in 3 to 4%, and echinoderms in only 1% of the fish in each size-group. The presence of the ctenophore *Beroe* in two stomachs in statistical rectangle K32 in July 1957 is worthy of note.

North Coast—Western Sector (Table XI)

In this region large cod were rather more numerous than the smaller fish from May to September in 1956 and 1957. In each size-group crustaceans were eaten more frequently than fish. Once again euphausiids were the commonest food of the smaller fish, while *Pandalus*, euphausiids and, to a less extent, *Hyas*, were the chief constituents of the food of the larger fish. The fish diet again consisted of a number of different species, in

TABLE XI

FOOD OF COD OFF THE NORTH COAST OF ICELAND—WESTERN SECTOR

GG32; HH30, 32

Years	1956–57				
Months	V–VII, IX				
Depth range m	99–130				
Length range cm	26–50	51–112			
No. stomachs examined	187	306			
No. empty	52 = 28%	88 = 29%			
No. with recognisable food	125 = 67%	200 = 65%			
No. with unrecognisable food	10 = 5%	18 = 6%			
Percentage feeding on:					
CRUSTACEA	73	63	PISCES	34	56
Decapoda ? sp.	2	1	*Gadus* ? sp.	—	4
Eupagurus	—	3	*G. aeglefinus*	4	7
Hyas	5	9	Flatfish ? sp.	1	1
Munida	1	—	*Hippoglossoides*	—	4
Pandalus	8	27	*Culpea harengus*	—	4
Hippolyte	—	2	*Anarhichas*	—	1
Pontophilus	—	1	*Sebastes*	—	2
Spirontocaris	—	1	*Lumpenus*	—	5
Euphausiacea	39	20	*Triglops*	1	1
Isopoda	1	1	MOLLUSCA	1	1
Amphipoda	1	1	Gasteropoda	—	1
POLYCHAETA	5	4	Lamellibranchiata	—	1
Aphrodite	—	1	ECHINODERMATA	4	13
Phyllodoce	1	—	Holothuroidea	2	5
Glycera	—	1	Ophiuroidea	2	8
			Echinoidea	—	1
			Asteroidea	—	1

which the haddock, in 7% of the stomachs, was the principal subtype. The complete absence of sand eels and capelin is of interest. Polychaetes and echinoderms were of some slight importance in the food of both size-groups but molluscs were eaten by only 1% of the fish.

CONSIDERATION OF RESULTS

While considering the seasonal variations in the intensity of feeding of cod at Iceland it has been shown that, from March to September, the proportions of fish with empty stomachs are greater than in Scottish and Faroese waters. This seems to indicate that at Iceland food is scarcer, or that the concentrations of cod are greater, so that the competition for food is more acute and the amount available for individual fish consequently smaller. Other factors relating to feeding must, however, be taken into account. For example, the nature of the food has been shown to include a bigger proportion of pelagic fish (capelin and sand eels) and other pelagic or semi-pelagic organisms (euphausiids and possibly other planktonic types) than in the Scottish and Faroese areas; this in turn may determine the feeding behaviour of the fish, whether daily or throughout the year, and perhaps also the digestion rates.

Consequently a more extensive study of the feeding of cod at Iceland would appear desirable to permit any definite conclusions in regard to the feeding intensity throughout the year.

The food of cod of 21 cm and over on Icelandic grounds consists predominantly of crustaceans and fish. Appreciable but much smaller quantities of molluscs, polychaetes and echinoderms are also eaten fairly regularly over the whole area, while nemerteans, gephyreans, small sponges, ascidians, anthozoans and ctenophores are eaten on rare occasions.

In addition to the identifiable food, the stomachs in four regions contained quantities of unrecognisable material. In view of the relative scarcity of unidentified food in the stomachs of Scottish and Faroese cod, this

feature has been examined in more detail at Iceland. In the Faxa Bay area, unrecognisable food was found on only one occasion, in July 1957, in the southern half of the bay itself. Similar food was also found in cod from most of the localities investigated off north-east Iceland and in both sectors of the north coast. Unidentified material occurred in from 3 to 6% of the stomachs of the cod of all sizes examined, but it is noteworthy that all these records were obtained in July 1957. A possible explanation of this material is that it represents predation on planktonic types which are quickly digested leaving no recognisable parts.

The proportions of the fish in the two size-groups feeding on the five principal food types are illustrated in Figure 2. This emphasises the prominence of crustaceans and fish in the cod's diet on all Icelandic grounds.

Crustaceans

Figure 2 also stresses the prominence of crustaceans in the diet of cod of 21–50 cm on Icelandic grounds generally, particularly in four of the seven regions, including the entire north and east coasts. A break-down of the crustacean food shows that most of it consists of decapods, particularly natant types, with *Pandalus* occurring more frequently in the stomachs than any other genus. Although in general the smaller cod tend to prey on *Pandalus* more frequently than the larger fish, this is not invariably so and on the north coast of Iceland predation on this genus was mainly by the larger size-group of cod. On the evidence available, predation on *Pandalus* over the area as a whole would appear to be heaviest from July to September, in which months this food type may occasionally be identified in as many as 75% of the stomachs.

Rather surprisingly, reptant decapods were found to be of much less importance to cod at Iceland than in Scottish and Faroese waters. In this group *Nephrops* and *Hyas* occurred most frequently in the stomach contents. *Nephrops norvegicus* was identified in the food in the outer reaches of both Brede Bay and Faxa Bay but the main concentrations of this animal on the basis of the contents of cod stomachs are clearly off the south coast from Reykjanes to the Oster Horn. Predation by cod on *Nephrops* was confirmed in this area in each month from March to September, although reaching a maximum intensity from June onwards when all the fish in certain samples were found to be feeding on this animal. As already demonstrated in the Scottish area (Rae, 1967a) *Nephrops* is eaten mainly by the larger cod.

Hyas was identified in the stomachs of fish of all sizes in five of the seven regions at Iceland and attained its highest overall frequencies of 13% in fish of 21–50 cm, and 15% in fish of 51 cm and over, in the north-western region, although it was eaten by as many as 18% of the smaller fish in the south-eastern region.

Another group of crustaceans which provides an important part of the diet of Icelandic cod is the *Euphausiacea*. These animals were eaten by cod in six of the seven regions and must be regarded as of major importance along the north and north-east coasts of Iceland. Considering the relatively small size of the individual euphausiids, and that in Scottish and Faroese waters they are rarely eaten by cod, and even then almost entirely by the smaller fish of 21–50 cm, one might have expected them to be preyed on mainly or entirely by the smaller cod at Iceland. This is not always so, however; Tables IX, X and XI show that euphausiids are eaten by 40%, 55% and 39% of the smaller fish and by 44%, 19% and 20% of the larger size-group off the north and north-east coasts. This group was identified in the food in April, May, July and September, but their incidence in the stomachs of the various samples suggests that their main importance as food of cod may be from May to July.

Fish

The importance of fish in the food of cod at Iceland is also demonstrated by Figure 2. In three of the seven regions, along the entire west and south-west coasts, fish represent the commonest food of both size-groups, and in Faxa Bay and the south-western region they may even exceed, both qualitatively and quantitatively, all the other groups combined. Moreover, in five of the seven regions and in Icelandic waters generally, fish provide the bulk of the food of the larger cod.

Of the individual fish types in the food of Icelandic cod, sand eels and capelin were of outstanding importance throughout the period of sampling, March to September. A study of the incidence of these two subtypes throughout the period, however, shows that capelin were eaten from March to July, but chiefly in March and April when they were taken by all the cod in certain samples. Meschkat (1936) also found cod

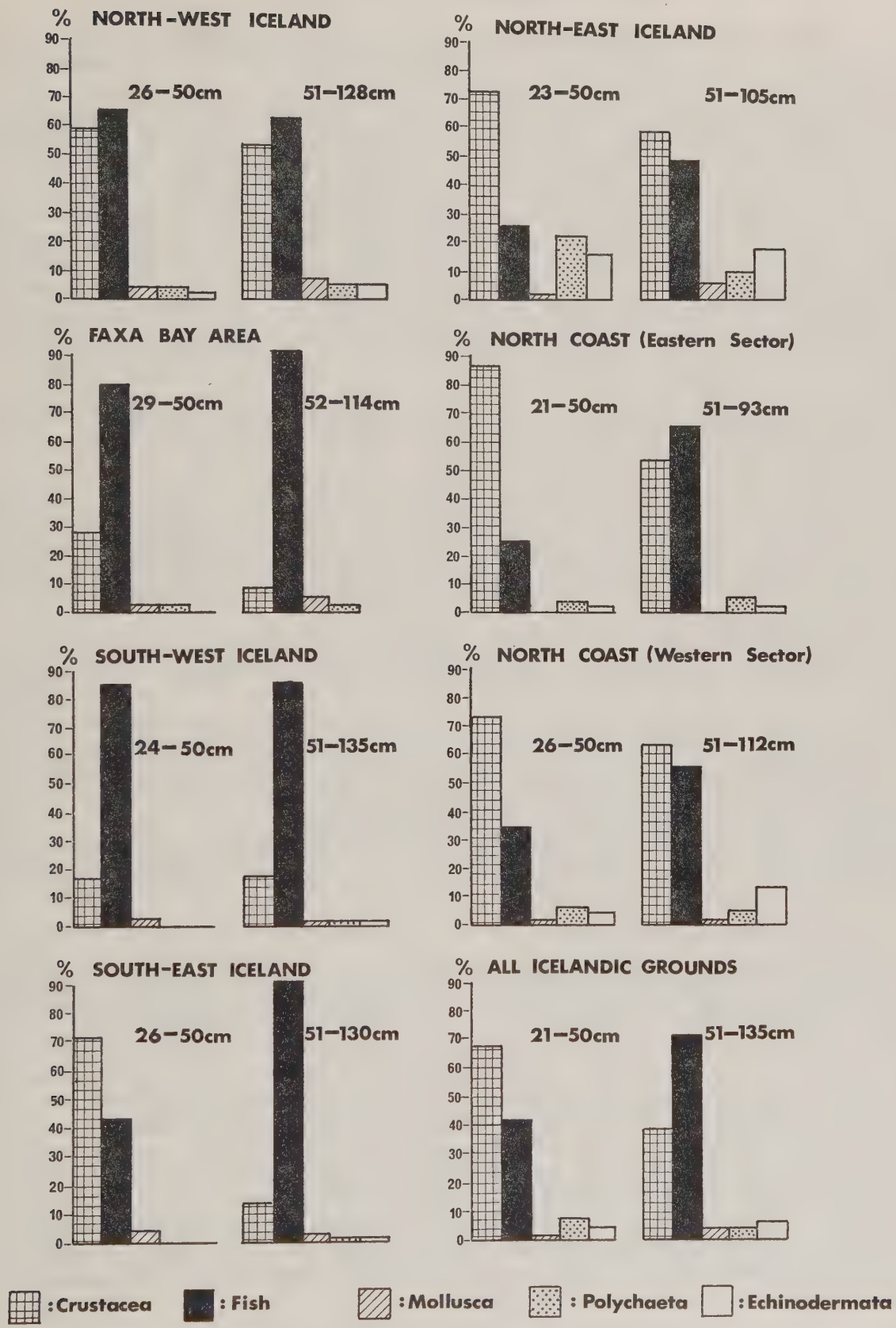

Figure 2. Frequency of occurrence of the five principal food types in cod stomachs at Iceland.

feeding on capelin in February 1935 near the Westmann Isles. Sand eels were identified in the food in March only once but their season is clearly from May to September, reaching a peak from July to September when they were eaten by up to 80 to 90% of the cod in individual samples.

These fish types were eaten over a wide area at Iceland but the capelin, a northern species, was rather surprisingly absent from stomachs in the north-western region and in the western sector of the north coast. This may, however, be owing to the failure to sample these regions before May in any year. Sand eels on the other hand were well represented in the cod food in the north-western region in May.

Sand eels and capelin are clearly the predominant food of cod in the Faxa Bay and south-western regions. Although sand eels would appear, from Tables VI and VII, to be of somewhat greater importance than capelin in these areas, this may be to some extent the result of the sampling. The complete absence of sand eels from stomachs collected in the south-eastern region from April to September in four different years, in which time capelin were observed in 74% of the stomachs of the larger cod, seems to suggest a regional difference in the food. Saemundsson (1949), however, records sand eels as very common on the south coast and common on the east coast, so that the absence of this food type from the cod stomachs off south-east Iceland is difficult to explain.

Both sand eels and capelin were rarely identified in the food of cod from north-east Iceland and from the eastern sector of the north coast and, as already stated, neither was found in the food in the western sector of the north coast from May to September of 1956 and 1957.

Cod in Icelandic waters also prey on a variety of other species of fish. Collectively the small gadoids come next in importance to sand eels and capelin. Whiting, blue whiting (*G. poutassou*), Norway pout (*G. esmarkii*), young cod and haddock were all identified, and of these Norway pout were eaten more frequently than any of the others, particularly on grounds stretching, in an anticlockwise direction, from north-west to south-east Iceland. Flatfishes, represented mainly by the long rough dab, were also eaten fairly regularly though much less frequently than the gadoids.

Herring were identified in the food in six of the seven regions, but only in 1 to 5% of the stomachs of the larger fish. In one sample of stomachs from the north coast the herring consisted of heads and other offal discarded from a processing vessel in the vicinity. The scarcity of evidence of cod preying on herring in Icelandic and Faroese waters is in sharp contrast to similar records from Scottish waters where these fish represent an important food of cod, locally and/or seasonally. It is possible, however, that samples from Icelandic coastal waters (within the three miles limit) would reveal cod feeding more frequently on young herring in nursery areas. Moreover, predation on adult herring at both Iceland and Faroe may be heavier in the deeper water beyond the areas sampled by Scottish research vessels.

As observed in previous studies of the food of the cod, the Icelandic investigations also confirm predation on various fish of little or no commercial value, both in coastal (e.g. *Lumpenus*) and offshore (*Lycodes*) waters.

Molluscs, Polychaetes and Echinoderms

As Figure 2 shows, these types in general are of relatively minor importance in the food of cod at Iceland and even collectively fall considerably short of either of the two major types. The molluscs are particularly unimportant compared with their incidence in the food of cod in Scottish and Faroese waters. This would seem to be to some extent owing to the comparative scarcity of cephalopods in the food at Iceland compared with Scottish waters and to a particularly intensive predation on *Buccinium* on certain Faroese grounds.

The greater frequency of polychaetes, particularly in the food of the smaller cod off north-east Iceland, and the relative scarcity of *Aphrodite* in Icelandic waters generally have already been noted.

The prevalence of echinoderms in the food of cod from north-east Iceland and, to a less extent, on the western sector of the north coast, has also been stressed. In Icelandic waters as a whole, as elsewhere, this group is mainly represented by the brittlestars (ophiuroids) but off north-east Iceland, holothurians were eaten by 13% of the smaller cod and 12% of the larger fish examined in the present investigations and thus would appear to be of greater importance to cod in this area than in any similar locality in any of the three major regions. The local incidence of holothurians and polychaetes in the diet of cod off north-east Iceland has previously been noted by Brown and Cheng (1946).

COMPARISON OF THE FOOD WITH THAT OF SCOTTISH AND FAROESE WATERS

Similarities and differences in the feeding habits and food of cod in Scottish, Faroese and Icelandic waters have already been noted throughout this report. It has been shown for example that the proportions of fish with empty stomachs at all times of the year are greater at Iceland than in either of the other regions. There is also evidence that the feeding cycle throughout the year is somewhat different at Iceland, although this is not altogether conclusive from the available data. On the other hand Trout's (1957) observations on the feeding of cod at Bear Island also seem to suggest a seasonal cycle which differs in some respects from the feeding cycles round Scotland and at Faroe—the main difference being the high proportions of empty stomachs from November to February at a time when feeding has been shown to be fairly active in both Scottish and Faroese waters. Unfortunately no sampling of cod stomachs was carried out by the Scottish research vessels at Iceland throughout the winter, but from the evidence of feeding at Iceland in August and September and again in March and April, some slight resemblance to the cycle in Arctic waters is detectable.

An interesting feature of the feeding cycle of cod is the spring decline immediately prior to the period of maximum intensity of feeding in June and July. In Scottish waters this occurs in the latter half of March and April and at Faroe in May. As already observed, this decline is not clearly marked at Iceland if based on the proportions of empty stomachs (Table I), but becomes more evident if the fullness of the stomachs is considered (Table IV). The annual feeding curve at Bear Island (Trout, 1957—Fig. 29) clearly indicates high percentages of cod with empty stomachs from the end of April to the beginning of June, so that the decline in feeding prior to the commencement of the main feeding season would seem to be characteristic of cod in all four regions. Although this decline has been linked with a possible cessation of feeding during the spawning season, this is not the complete explanation as the feeding of immature cod has also been seen to fall away in Scottish and Faroese waters (Rae, 1967a, b) and evidently also at Bear Island, although here the comparison is not so satisfactory owing to the extensive migrations of young cod in this region. Only at Iceland do the young cod appear to maintain a steady intensity of feeding throughout the spring and summer, but here further sampling would seem desirable to clarify both the spring decline and the intensity of feeding throughout the winter months.

The percentages of fish in the two size-groups feeding on the five principal food types are given in Table XII. This stresses the overall importance of crustaceans and fish in all three regions. Table XII also indicates the predominance of crustaceans in the diet of the smaller cod of 21–50 cm and of fish in that of the larger size-group of 51 cm and over. It also demonstrates the relatively minor and variable roles of molluscs, polychaetes and echinoderms in the food in all three regions. For example, cod of all sizes clearly prey more frequently on molluscs at Faroe than in the other two regions while predation on this group is at its lowest at Iceland. Polychaetes appear to be eaten more frequently by small cod at Iceland (particularly in the north-eastern region) and by the larger fish in Scottish waters where *Aphrodite* is an item of some importance. Finally, echinoderms represent an appreciable part of the food of all sizes of cod in some Icelandic and Faroese waters but are of negligible value in the North Sea. Despite their relative unimportance, on average, the three minor food types not infrequently attain a much greater importance on local grounds.

The relative importance of the principal subtypes within each of the five chief food groups in each region

TABLE XII

PERCENTAGES OF COD FEEDING ON CHIEF FOOD TYPES ON SCOTTISH, FAROESE AND ICELANDIC GROUNDS

	21–50 cm			51 cm and over		
	Scotland	Faroe	Iceland	Scotland	Faroe	Iceland
Crustacea	62·0	62·5	67·6	50·0	34·0	38·4
Pisces	54·0	47·2	42·3	66·0	76·8	71·4
Mollusca	2·7	13·8	1·2	4·4	14·9	2·6
Polychaeta	2·5	3·1	7·0	5·0	2·2	3·3
Echinodermata	0·5	3·4	4·6	1·7	4·4	5·3

TABLE XIII

RELATIVE IMPORTANCE OF CHIEF SUB-TYPES IN COD FOOD ON SCOTTISH, FAROESE AND ICELANDIC GROUNDS

	Scotland	Faroe	Iceland
Eupagurus	+ + +	+ +	+
Portunus	+ + +	+ +	+
Hyas	+ +	+ +	+ +
Nephrops	+ + +	—	+ +
Pandalus	+ + +	+ + +	+ + +
Euphausiids	—	—	+ + +
Sandeels (*Ammodytes*)	+ + +	+ + +	+ + +
Capelin (*Mallotus*)	—	—	+ + +
Whiting	+ +	+	+
Haddock	+	+ +	+
Norway pout	+	+	+ +
Herring	+ +	+	+
Cephalopods	+	—	—
Buccinum	+	+ +	—
Aphrodite	+ +	+	+
Ophiuroids	—	+	+

Key: + + + of major importance
+ + of moderate importance
+ of slight importance
— absent or of negligible importance

These estimates of the relative importance of the various food items may be regarded as averages for each region; it should be noted that some types may be of greater or less importance locally or seasonally.

is indicated in Table XIII. This stresses the similarities and differences in the food from one region to another. The food in Scottish and Faroese waters has already been compared briefly (Rae, 1967b), so that the distinctive features in Icelandic waters remain to be identified. Of the 16 subtypes listed in Table XIII, sand eels and pandalids are of major importance in all three regions, and while some organisms are of moderate importance in each region, others vary considerably in their frequency of occurrence in the stomachs from one region to another. It is noteworthy that of the four major constituents of the food at Iceland (*Pandalus*, Euphausiacea, sand eels and capelin) two are either absent or are of negligible importance in Scottish and Faroese waters. The first of these, the capelin, has never been recorded in the British marine fauna, and although this fish has been found at Faroe (Saemundsson, 1949) it has not been recorded in the food of cod there. Saemundsson has emphasised the very great importance of the capelin as cod food at Iceland. The second major subtype is the Euphausiacea, represented largely it would seem by *Meganyctiphanes norvegica*. Euphausiids are rarely eaten by cod of 21 cm and over in Scottish and Faroese waters, so that their frequency in the stomachs of cod of both size-groups at Iceland is a major difference which suggests some peculiarity in the mode of feeding at Iceland, particularly off the north and north-east coasts. The presence of these two subtypes in the food of cod at Iceland stresses the resemblance to the pelagic or near-pelagic feeding of this fish in Arctic waters (Trout, 1957).

Moreover, the occurrence of appreciable quantities of unrecognisable material in the stomachs at Iceland also points to predation on some unknown organisms, possibly ctenophores, which disintegrate quickly under the influence of gastric fluids, leaving no recognisable resistant parts. Although in the present investigation *Beroe* was found in the stomachs of only two cod from north of Iceland, ctenophores and other pelagic invertebrates are known to be eaten by cod in the Arctic (Jensen and Hansen, 1931; Graham *et al*, 1954).

While the food of cod at Iceland resembles that of Scottish and Faroese waters, both in its general composition and in the individual species preyed on, the geographical situation of the three regions clearly presupposes the gradual disappearance of southern species, for example, *Corystes*, *Gonoplax*, *Clupea sprattus* and *Solea*, from the food and the appearance of more northerly forms, such as *Sabinea*, *Lithodes*, *Mallotus* and

Lycodes, as one proceeds northwards from the North Sea to Iceland. Moreover, the supreme importance of *Mallotus* and euphausiids in the food at Iceland and the possible predation on other pelagic species, such as ctenophores, clearly emphasises the affinities of the food at Iceland with that of truly Arctic regions. Iceland would, therefore, appear to occupy an intermediate position in the food of cod between the boreal regions of the North Sea and Faroe and the Arctic regions represented by Bear Island. In this respect it bears a remarkably close resemblance to the Gulf of St Lawrence where the food of cod has been investigated by Powles (1958). Not only does food in the Gulf of St Lawrence consist predominantly of crustaceans and fish with smaller quantities of molluscs, polychaetes and echinoderms, but prominent features include capelin, euphausiids, natant decapods, and to some extent ctenophores and other planktonic types.

SUMMARY

This study of the food of cod in Icelandic waters is based on the examination of the stomach contents of nearly 3,000 cod of 21 cm and over caught by Scottish research vessels from 1952 to 1958. Sampling was confined to the months March to September, so that the section of the feeding cycle during the winter has not been determined. Feeding is heaviest in June and possibly in July and there is some evidence of a marked decline in May immediately prior to the commencement of intensive feeding. The proportions of empty stomachs is greater at Iceland than in either of the Scottish or Faroese areas.

The food consists predominantly of crustaceans and fish, with smaller quantities of molluscs, polychaetes and echinoderms. The smaller fish in some localities prey more on crustaceans and the larger cod on fish, but in other localities, for example Faxa Bay and the south-west coast, fish constitute the chief food of all sizes of cod above 21 cm.

The outstanding individual food types in the Icelandic region as a whole are sand eels, capelin, *Pandalus* and euphausiids, while *Nephrops* are of considerable importance off the south coast, and polychaetes, ophiuroids and holothurians are eaten fairly frequently off north-east Iceland.

Comparison is made with the food of cod in other regions. Many genera and species are common to Scottish, Faroese and Icelandic grounds, but capelin are peculiar to the food at Iceland, while euphausiids, which form an insignificant part of the food in Scottish and Faroese waters, represent one of the major items in the cod's diet along the north coast of Iceland.

Another feature of the Icelandic investigations, not observed in Scottish and Faroese waters, is the appreciable proportion of stomachs containing unrecognisable material. This is most noticeable along the north coast and may possibly indicate predation on ctenophores or other planktonic types. The prominence of capelin and euphausiids in the cod food stresses the intermediate position of Iceland between the boreal regions of Faroe and Scotland and the Arctic as represented by Bear Island.

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Appendix

List of Genera and Species identified in the Food of Cod, in Icelandic Waters, with Place of Occurence indicated by Statistical Rectangle

(see Figure 1)

CRUSTACEA

DECAPODA – REPTANTIA

Eupagurus sp.: DD29; EE31, 32; GG26, 32; HH30, 32; KK32; PP31, 32; RR28, 30.
Portunus sp.: EE27; HH26; NN27.
Hyas sp.: CC30, 31; DD29, 30; EE31, 32; GG32; HH30, 32; KK32; LL31; MM32; NN27; PP31, 32; QQ31; RR28, 30.
H. araneus (L.): DD29, 30; EE31.
H. coarctatus Leach: PP32.
Lithodes maia (L.): CC30.
Nephrops norvegicus (L.): DD29; EE26, 27; FF26; GG25, 26; HH25; LL25, 26; PP27.
Galathea sp.: DD29; EE32; HH25.
Munida sp.: CC30, 31; EE31; FF27; HH30; MM26.

DECAPODA – NATANTIA

Crangon sp.: CC30, 31; DD29, 30; EE26, 31, 32; FF26, 27; GG26; JJ25; LL31; NN27; PP32; RR30.
C. allmani Kinahan: DD29; GG26.
Pandalus sp.: CC31; DD27, 29, 30; EE26, 31, 32; FF26, 27; GG26, 32; HH26, 30, 32; KK32; LL25, 26, 31; MM26, 32; NN27; PP27; QQ29.
P. montagui Leach: DD29; EE26; FF27.
P. borealis Krøyer: LL26.
Pontophilus sp.: EE31; HH30; LL31; MM32; PP31.
Sclerocrangon sp.: RR30.
Hippolyte sp.: EE27, 31; GG32.
Spirontocaris sp.: DD29, EE31; HH32.
Sabinea sp.: PP31.

EUPHAUSIACEA

Meganyctiphanes norvegica M. Sars: HH26; MM26, 32.
Thysanoessa inermis (Krøyer): PP31; QQ29.

ISOPODA

Calathura brachiata Stimpson: LL31.
Aega psora (L.): PP32.

AMPHIPODA

Rachotropis aculeata (Lepechin): MM32.
Tmetonyx sp.: MM32.
Eusirus cuspidatus Krøyer: QQ31.
Themisto sp.: GG32.

PISCES

Ammodytes spp.—sand eels: CC31; DD29, 30; EE31; FF26, 27; GG26; HH25, 26; JJ25; MM32; RR30.
Mallotus villosus (O. F. Muller)—capelin: EE26; FF26, 27; GG26; HH26; JJ25; KK25; LL26; MM26, 32; PP27; QQ31.
Gadus spp ?—gadoids: DD29; EE31; GG32; HH32; MM26, 32; PP31; QQ29; RR28.
G. aeglefinus L. = *Melanogrammus aeglefinus*—haddock: EE27; HH32; QQ29.
G. merlangus L. = *Merlangius merlangus*—whiting: DD30; EE31; QQ29.
G. esmarkii Nilsson = *Trisopterus esmarkii*—Norway pout: CC31; DD29; EE31; GG25, 26; HH25; JJ25; MM26; NN27; QQ29.
G. poutassou (Risso) = *Micromesistius poutassou*—blue whiting: DD28; GG25, 26; JJ25; MM26; QQ27.
G. callarias L. = *G. morhua*—cod: PP31; RR28.
Clupea harengus L.—herring: DD28; EE27; FF26; GG32; HH32; JJ25; KK25; MM31; PP32.
Flatfish ? sp.: DD29; EE31; GG26, 32; HH30; LL25, 26, 31; MM26, 31; PP31; QQ29.
Hippoglossoides platessoides (Fabricius)—long rough dab: CC31; EE26, 31, 32; FF26; GG25; HH26, 30; KK32; LL31; MM26; PP31; QQ29.
Sebastes sp.: GG32; HH32.

Lumpenus sp.: EE31; HH30; LL26, 31; MM32; PP31, 32; QQ29.
Argentina sp.: GG26.
Triglops sp.: GG32; KK32; LL31; RR28.
Anarhichas sp.: GG32; HH32; QQ31; RR30.

Lycodes sp.: KK32; LL31; RR28.
Onos cimbrius (L.)—four-bearded rockling: LL25.

MOLLUSCA

GASTEROPODA

Buccinum sp.: DD30.

LAMELLIBRANCHIATA

Modiolus sp.: DD29.
Anomia sp.: EE31.
Astarte sp.: MM26.
Pecten sp.: QQ27.

POLYCHAETA

Aphrodite aculeata (L.): EE27, 31; GG26; HH30; LL25, 31; RR30.
Phyllodoce sp.: HH32.
Glycera sp.: HH32.

ECHINODERMATA

OPHIUROIDEA

Ophiopholis aculeata (L.): DD29; HH32; QQ31.
Ophiura texturata Lamarck: QQ31.

ASTEROIDEA

Hippasterias sp.: HH30.

CTENOPHORA

Beroe sp.: KK32.

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